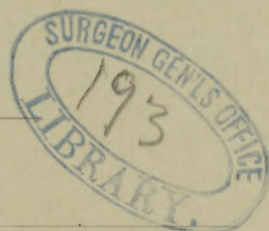


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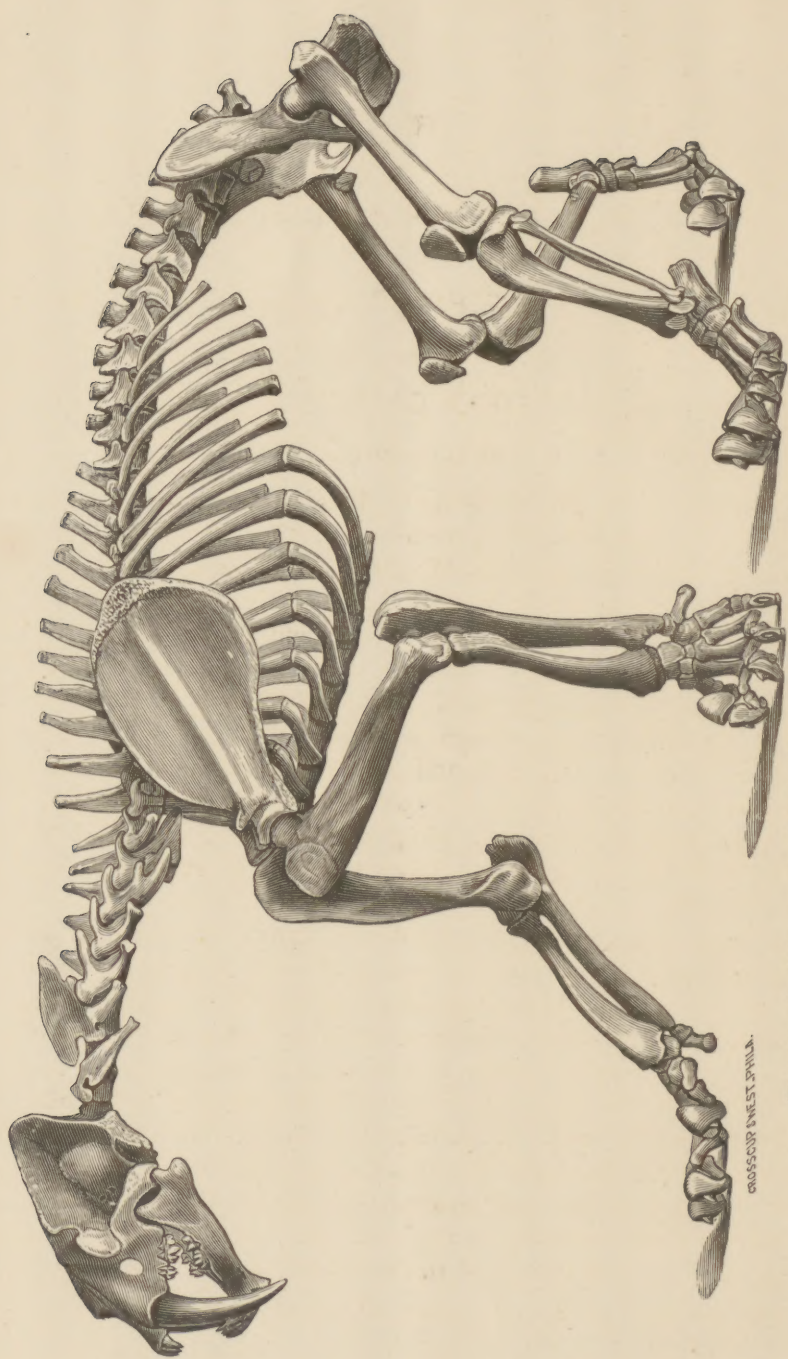
ON THE
Extinct Cats of America.

BY
E. D. COPE.

From the American Naturalist, for December, 1880.







CROSSOUR INEST SPINA.

FIG. 12.—*Smilodon necator* Gervais, less than one-ninth natural size. From Burmeister.

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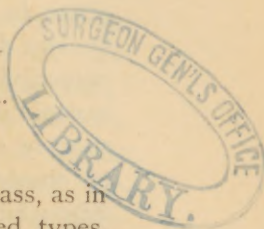
ON THE EXTINCT CATS OF AMERICA.

BY E. D. COPE.

IN following the general series of the *Carnivora*, we pass, as in other orders, from the generalized to the specialized types. That we should begin with the *Procyonidæ* (raccoons) and their allies, is indicated by all the characters to be especially considered in the case. They have five toes on all the feet and are plantigrade, resembling in these points all primitive *Mammalia*.¹ They have the original number of molar teeth, seven on each side, and of these none are distinctly developed sectorials. The condyloid and carotid foramina are distinct, and there is a postglenoid foramen. If, starting from this point of departure, we arrange the succeeding families of *Carnivora* according to their resemblances and differences in these respects, we have a tolerably consecutive series of divisions.

Passing at present over the families *Mustelidæ*, *Viverridæ*, *Cryptoproctidæ* and others, with five toes on all the feet, we reach those in which the hind foot has lost a digit, leaving the number 5—4. These are the *Protelidæ*, *Canidæ* and *Felidæ*. We can take but one step further in this order, that is, to those species where the anterior foot has also lost a toe, which constitute the family *Hyænidæ*. The toes are therefore here 4—4. For the well-marked characters of the three families mentioned just before, I refer to another page, and proceed to define, briefly, the division which has been heretofore termed the *Felidæ*. In doing so I am compelled to omit several of the characters generally employed

¹ See Homologies and Origin of Types of Molar Teeth of *Mammalia educabilia*. Journal Academy Phila., 1874, March.



to define that family, since I have found them to be wanting from various extinct genera. The only comprehensive definition which I can give is the following:

Digits 5—4. Sectorial teeth well developed in both jaws; not more than one true molar tooth in the upper, nor more than two true molar teeth in the lower jaw. Glenoid cavity grasping mandibular condyle anteriorly as well as posteriorly.

Prof. Gill, who has devoted much attention to the definition of the families of the *Mammalia*,¹ gives the following skeletal characters in his diagnoses of the *Felidæ* and of the three comprehensive divisions within which he places it. "I. Skull with the paroccipital process applied closely to the auditory bulla; the mastoid process small or obsolete; external auditory meatus very short or imperfect. Div. A. Carotid canal minute and superficial or obsolete; condyloid foramen and foramen lacerumposticum debouching into a common fossa; glenoid foramen minute or null. Os peuis rudimentary. Subdiv. 1. Otic bulla divided by a septum into posterior and anterior chambers communicating by a narrow aperture (Flower). Subdiv. a. Skull with no alisphenoid canal." All of the parts here mentioned I have found to be important in the definition of the natural divisions of the *Carnivora*, excepting those derived from the paroccipital and mastoid processes. But their condition in the extinct *Carnivora* which have been hitherto arranged with the *Felidæ*, and which resemble them very much in superficial characters, does not coincide with Prof. Gill's definition. Thus in the various American genera which resemble *Drepanodon*, the carotid canal is distinct from the *foramen lacerum posterius*, and the condyloid foramen is also separated from it by quite a space. These are characters which belong to most of the *Carnivora* with five digits on all the feet. Further, the postglenoid and postparietal foramina are present, also characters of the lowest *Carnivora*, as the bears and certain extinct dogs. Then there is an alisphenoid canal, which is also found in bears, dogs and the cat-like *Cryptoprocta*. I cannot demonstrate that the otic bulla is divided as the above diagnosis requires, in any of the fossil species. I have verified the above characters on species of the following genera, of which I have well preserved skulls; *Archælorus*, *Nimravus*, *Dinictis*, *Pogonodon*,²

¹ Arrangement of the Families of Mammals. Smithson. Miscell. Coll., 230, 1872, p. 56.

² Except those of the base of the skull.

and *Hoplophoneus*. Three genera, as yet only found in Europe, are similar in general characters, and probably agree with them. I allude to *Proaelurus* Filh., *Ælurogale* Filh., and *Eusmilus* Gerv. On the other hand, the genus *Smilodon*, which includes the American sabre-tooths of Pliocene age, agrees with the true cats in the points in question; *i. e.*, the alisphenoid, postglenoid and postparietal foramina are wanting; the carotid foramen is either internal or wanting, and the condylar enters the jugular foramen at its mouth. This surprising condition of affairs makes it important to learn the characters to be found in the species of the longest known genus, *Drepanodon*, of the European beds. But although there are several good crania in European museums, I can find no description of their minute characters, and no mention made of their foramina. The probabilities are, on various grounds, that this genus agrees with *Smilodon* in the latter characters. The reasons in favor of this supposition are, the agreement in special dental characters, and the Pliocene age of the typical species, *D. cultridens*. Whether the Miocene species of Sanzan and Epplesheim agree with this one in structure, is of course uncertain.

Seven and perhaps eight genera then, constitute a group to be distinguished from the true *Felidæ*, and, as it appears to me, as a distinct family. Should we ignore the characters adduced in this instance, we abandon at the same time the definitions of several of the other families of the order, and in fact, throw the system into confusion. I have proposed to call this family the *Nimravidæ*, and have contrasted it with the *Felidæ* in the following definition. Both are included in the division already defined on a preceding page.

No distinct carotid foramen nor alisphenoid canal;
condylar foramen entering the foramen lacerum
posterius. No postparietal, and generally no post
glenoid foramina;

Felidæ.

Carotid and condylar foramina entirely distinct from
the foramen lacerum posterius; an alisphenoid
canal, and post glenoid and postparietal for-
amina;

Nimravidæ.

NIMRAVIDÆ.

The dental characters of the *Nimravidæ* are in general those of the *Felidæ*, the higher genera having the same dental formula,

Descending the scale the number of molar teeth increases at both ends of the series in the lower jaw, and anteriorly only in the upper, the number of the true molars never exceeding $\frac{1}{2}$. The following table gives the definitions of the genera. I am unfortunately ignorant of the characters of the foramina in *Proælurus* and *Pseudælurus*, as well as in *Ælurogale* and *Eusmilus*.

I. Lateral and anterior faces of mandible continuous; no inferior flange.

a. No anterior basal lobe of superior sectorial; inferior sectorial with a heel; canines smooth.

Molars $\frac{4}{3} \frac{1}{2}$; inferior sectorial with interior tubercle.....*Proælurus*.

Molars $\frac{3}{3} \frac{1}{2}$; inferior sectorial without interior tubercle.....*Pseudælurus*.

II. Lateral and anterior faces of mandibles separated by a vertical angle; no inferior flange; incisors obspatulate.

a. No anterior basal lobe of superior sectorial; inferior sectorial with a heel (and no internal tubercle); incisors truncate.

Molars $\frac{4}{3} \frac{1}{2}$; canine smooth.....*Archælurus*.

Molars $\frac{3}{3} \frac{1}{2}$; canine denticulate.....*Ælurogale*.

Molars $\frac{3}{3} \frac{1}{2}$; canine denticulate.....*Nimravus*.

III. Lateral and anterior faces of mandible separated by a vertical angle; an inferior flange; incisors conic, canines denticulate.¹

a. No or a small anterior basal lobe of superior sectorial;² inferior sectorial with a heel. No posterior lobes of the crowns of the premolars.

Molars $\frac{3}{3} \frac{1}{2}$*Dinictis*.

Molars $\frac{3}{3} \frac{1}{2}$*Pogonodon*.

Molars $\frac{2-3}{2} \frac{1}{2}$*Hoplophoneus*.

Molars $\frac{?}{1} \frac{?}{1}$*Eusmilus*.

It is readily perceived that the genera above enumerated form an unusually simple series, representing stages in the following modifications of parts: (1) In the reduced number of molar teeth. (2) In the enlarged size of the superior canine teeth. (3) In the diminished size of the inferior canine teeth. (4) In the conic form of the crowns of the incisors. (5) In the addition of a cutting lobe to the anterior base of the superior sectorial tooth. (6) In the obliteration of the inner tubercle of the lower sectorial; and (7) in the extinction of the heel of the same. (8) In the development of an inferior flange and lateroanterior angle of the

¹ Gervais' figures of the canines of *Eusmilus bidentatus* represent no denticulations, but the figure is not clear.

² Rudimental in *Hoplophoneus*.

front of the ramus of the lower jaw. (9) In the development of cutting lobes on the posterior borders of the larger premolar teeth.

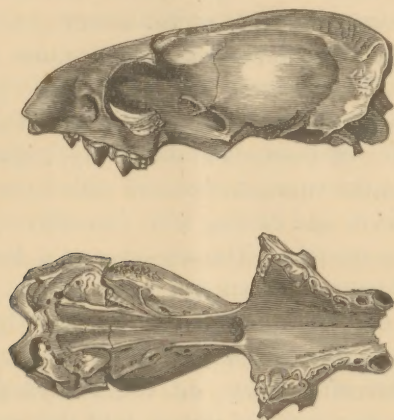


FIG. 1.—*Proaelurus julieni* Filh.; two-thirds nat. size. From Filhol.

(1) The reduction in the number of molar teeth. The dental formula of *Proaelurus* is that of some *Viverridæ* and *Canidæ*, and the reduction from this point to the end of the series is obvious. In *Eusmilus*, as in *Smilodon*, the number of molars is less by one in the inferior series, than in *Lynx* and *Neofelis*, where the formula is the smallest known among *Felidæ* proper, viz: $\frac{2}{2} \frac{1}{1}$.

(2) The enlarged size of the superior canine teeth. In *Proaelurus* and *Pseudaelurus*, the canines of both jaws are subequally developed as in recent *Felidæ*. In *Archaelurus* the superior is the larger, but does not, relatively to the molars, exceed that of *Felis*. It is rather compressed in form, and has



FIG. 2.—*Proaelurus julieni* Filh.; two-thirds nat. size; *a* inner view of mandible; *b* superior view of inferior teeth; *c* inferior sectorial, natural size. From Filhol.

a sharp cutting edge posteriorly. In *Nimravus* the superior canine begins to have the enlarged size of the sabre-teeths, but its form is peculiar in the *N. gomphodus*, being spike-shaped rather than sabre-shaped. We find the true sabre-shape first in *Dinictis*, where it is compressed, and with a denticulate cutting edge on both front and rear. In *Pogonodon* it has reached a very large size, and it does not display much increase in this respect until we reach the last genus of the series,

Eusmilus, where its proportions are enormous; almost as large as in the feline genus *Smilodon*, where they appear to have been an inconvenience to the animal. (3) The diminished size of the inferior canines becomes evident in the lower genera of the third division (supra) of the *Nimravidæ*, but is most decided in the highest genera *Hoplophoneus* and *Eusmilus*. (4) The incisor teeth have the usual obspatulate or obovate outline in the genera of the first and second divisions of the family, including *Nimravus*. They are conic in the true sabre-teeth with flared lower jaw, beginning with *Dinictis* and ending with *Eusmilus*. (5, 6 and 7) The structure of the sectorials. The presence of a heel and an inner tubercle of the lower sectorial are well known characters of a majority of the *Carnivora*. In only the most highly organized genera are they wanting, and among them are included all those of the *Felidæ* that still exist. In the *Nimravidæ* the inferior genera have both in a reduced degree, and they soon disappear as we ascend the scale. Thus the inner tubercle is only present in the species of *Proælurus*, *Dinictis* and *Hoplophoneus*. The heel on the other hand remains throughout the entire family. The anterior basal lobe of the superior sectorial has the same history, its absence being characteristic of the inferior *Carnivora*, and of all the genera of *Nimravidæ*, except in *Hoplophoneus*, where it is rudimental. It is well developed in *Drepanodon*, as in recent *Felidæ*, and is double in *Smilodon neogaeus*. (8) The development of the inferior flange and lateroanterior angle of the mandibular ramus. There is a successive advance in the development of these characters, beginning with the second group, for in the first they are wanting. The lateroanterior angle is developed in *Archælurus* and allied genera, and is merely continued on the inferior border of the ramus. In the third group it is much more acute, and is deflected downwards, forming the well known flange of the sabre-teeth. It is longest in the *Eusmilus bidentatus* Filh. (9) The highest genera of *Nimravidæ*, e. g. *Hoplophoneus*, differ from the true *Felidæ*, in the absence of the cutting lobes on the posterior edges of the crowns of the larger premolar teeth. But according to Filhol these lobes are present in the generalized genera, *Proælurus* and *Pseudælurus*, which are thus brought into a relation with the *Felidæ*, not possessed by other *Nimravidæ*.

A characteristic perfection of the *Felidæ* is seen in the genus *Smilodon*; that is, the vertical direction of the ungual phalanges, by

which the claws become retractile. This is well displayed by the two splendid specimens of *Smilodon necator* from Buenos Ayres, which have been preserved (See Fig. 12). Unfortunately, these phalanges have not yet been discovered in any species of the *Nimravide*, and it is not yet certain what their structure really was. Among the true *Felide*, the genus *Cynaelurus* displays a less degree of development in this respect than the other genera, the ungual phalanges lacking the proximal process below the articular facet. Such a condition is to be looked for among the less perfect genera of *Nimravide*.

The succession of genera above pointed out coincides with the order of geologic time very nearly. Those belonging to groups first and second, belong to the lower and middle Miocene, except *Ælurogale*, which is perhaps upper Eocene, and *Pseudaelurus*, which is middle Miocene. The genera of the first group of division third, have the same lower Miocene age, except *Eusmilus*, which has been found in the same formation (Phosphorites) as the *Ælurogale*.

The relations of these genera are very close, as they differ in many cases by the addition or subtraction of a single tooth from each dental series. These characters are not even always constant in the same species, so that the evidence of descent, so far as the genera are concerned, is conclusive. No fuller genealogical series exists than that which I have discovered among the extinct cats.

As to the phylogeny of this family, there are flesh-eaters of the Eocene period which may well have been the ancestors of both the *Nimravide* and *Felide*.¹ I have suggested that this position is most appropriately held by the *Oxyenide*, a family of several genera, which included the most formidable rapacious mammals of that early period in both continents. The interval between them and the *Nimravide* is however great, for in the *Oxyenide* when there is a sectorial tooth of the upper jaw, the first true molar is utilized instead of the last premolar; and the second true molar below is a sectorial as well as the first. Several intervening forms must yet be found to complete the connection, if it have ever existed. It is, however, very likely that the true *Felide* were derived from the genus *Proaelurus* through *Pseudaelurus*, if indeed these two genera be not the primitive members of that family, for as above

¹ See, On the genera of the *Credonta*, by E. D. Cope, Proceed. Amer. Philos. Soc. July, 1880.

remarked, the evidence of their possession of the characters of the *Nimravidae* has not yet been obtained. There can be no reasonable doubt that the genera *Drepanodon* and *Smilodon* in the *Felidae* are the descendants of *Hoplophonus* and allied genera. In fact, the *Nimravidae* and *Felidae* are "homologous groups," having corresponding terms in the manner I foreshadowed as a general principle in 1868 (Origin of Genera).

In looking for causes in explanation of the modifications of structure cited, one can easily discover that there is a close relation between the arrangement of the teeth and the mechanical laws involved in the performance of their function, those of seizing an active prey, and of cutting up their carcasses into pieces suitable for swallowing. It is obvious that in the latter case the flesh teeth bear the resistance, and the masseter muscle is the power, and that the nearer these parts are together, the better is the function performed. As a matter of fact, the sectorial teeth in modern carnivora are placed exactly at the angle of the mouth, which is the front border of the masseter muscle.

In the process of evolution both the muscle and the teeth have moved forwards in connection with the shortening of the jaw behind. This has been due to the necessity of bringing the power (masseter) nearer to another point of resistance, viz: the canine teeth.

In the early carnivores (as Hyænodontidae) the long jaws supported more numerous teeth ($\frac{1-3}{1-3}$) than in any modern families, and the fissure of the mouth was probably very wide, as the last molar was a sectorial. The canine teeth were evidently very ineffective weapons. The animals probably only snapped with their jaws, and did not attempt to lacerate or hold on, as do the cats.

The dogs of to-day are long jawed, and they snap in a manner quite distinct from anything seen among the cats. The only dogs that hold on are the short jawed bull-dogs.

So in the use of the canines we have the ground of the shortening of the jaw behind and before, and the consequent change of structure which resulted in the modern perfected *Felidae*.¹

The following list shows the number and distribution of the species of the *Nimravidae*:

¹ See AMERICAN NATURALIST, 1878, p. 171.

	Upper Eocene.	Lower Miocene.		Upper Miocene.		Pliocene.	
		Eur.	Am.	Eur.	Am.	Asia. Eur.	Am.
<i>Proælus julieni</i> Filh		×					
“ <i>lemanensis</i> Filh.....		×					
<i>Pseudælus hyænoide</i> Blv.....				×			
“ <i>edwardsi</i> Filh.....	×						
“ <i>intrepidus</i> Leidy.....					×		
“ <i>sivalensis</i> Lydd.....						×	
<i>Archælus debilis</i> Cope.....			×				
<i>Ælurogale intermedia</i> Filh.....	×						
“ <i>“acutata</i> Filh.” ¹							
<i>Nimravus gomphodus</i> Cope.....			×				
“ <i>confertus</i> Cope.....			×				
<i>Dinictis felina</i> Leidy.....			×				
“ <i>cyclops</i> Cope.....			×				
“ <i>squalidens</i> Cope.....			×				
<i>Pogonodon platycopis</i> Cope.....			×				
“ <i>brachyops</i> Cope.....			×				
<i>Hoplophoneus oreodontis</i> Cope.....			×				
“ <i>primævus</i> Leidy.....			×				
“ <i>occidentalis</i> Leidy.....			×				
“ <i>cerebralis</i> Cope.....			×				
<i>Eusmilus bidentatus</i> Filh.....	×						

We may now consider in more detail the characters of the genera and species of North America.

Division I. The Primitive Cats.

PSEUDÆLURUS Gervais. Although this genus commences in the Phosphorites of France, which are generally referred to the upper Eocene, it has at least some dental characters of the true *Felidae*. Even at that early period, if well defined period, it be,² the premolar teeth are lobed; see *P. edwardsi* Filhol. The single American species, the *P. intrepidus* Leidy is from a late Miocene formation, the Loup Fork. It is only known from lower jaws, of which Dr. Hayden procured one in Nebraska, and the writer another in Colorado. It was a species with large teeth, of about the size of the Canada lynx.

Division II. The False Sabre-teeths.

ARCHÆLURUS Cope.

This genus is of interest as completing the connection between the sabre-tooth and primitive unspecialized groups of the cats, a transition also clearly indicated by the genus *Nimravus*. In den-

¹ I only know this species by name.

² The Phosphorites are suspected by some to contain mixed materials from different horizons.

tition it adds a tooth to the number belonging to that genus, in both jaws, and has a smooth-edged canine; it is otherwise identical with that genus, unless, indeed, the exostosis supporting the inferior sectorial tooth in the *A. debilis*, be introduced into this category; a position I am not prepared to assume positively. There is but one species known, the

Archæolurus debilis Cope.

It is probable that this was an animal presenting much the appearance of the existing cats, and of about the size of the American panther. Omitting more technical characters, it differed from this and other species of the *Felidae* in the greater slenderness of its feet. Its head was characterized by less breadth through the posterior part of the cheeks, and by a greater convexity of the forehead between the eyes, and a greater prolongation backwards of the same region.

Its structure plainly indicates that this species was of less sanguinary habits than the existing *Felidae*, since its prehensile organs, both of the feet and dentition, are less robust. The slender zygomata and rami of the lower jaw show also that the impact of its bite was less powerful, although the large size and narrow form of the sectorial teeth, furnish an effective cutting apparatus, which in some degree supplements the deficiency of strength. The weakness of the rami is further provided against

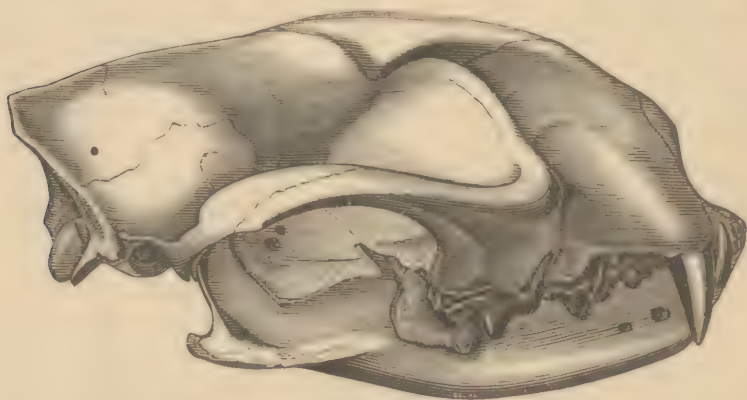


FIG. 3.—*Archæolurus debilis*, one-half natural size. Mus. Cope. From Vol. IV, Report of U. S. Geol. Surv. Terrs.

by the curious exostosis at the base of the inferior sectorial, already mentioned; see Fig. 3.

The first description of this species was given by myself under the head of the *Nimravus brachyops* (*Machærodus brachyops*, Palæontol. Bulletin, 30, p. 10, Dec., 1878), from a skull found by

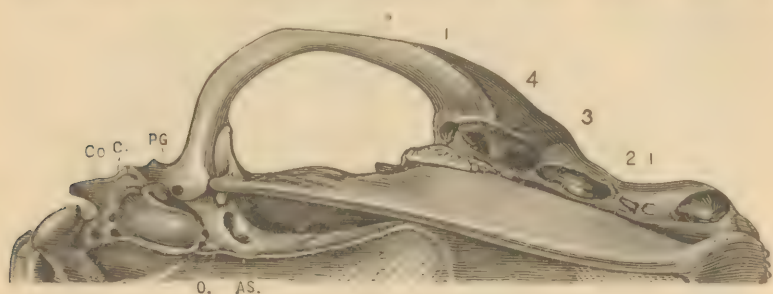


FIG. 4.—*Archæolurus debilis*, one-half nat. size; inferior aspect of Fig. 1. Foramina: AS, alisphenoid; O, ovale; PG, postglenoid; C, carotid; Co, condylar.

Mr. Sternberg, under the impression that it might belong to a female of that species. Subsequently a nearly perfect cranium, obtained by Mr. Wortman, demonstrated the distinctness of the animal both as to species and genus.

Horizon and Locality. The remains of the *Archæolurus debilis* have so far been only found in the Truckee Miocene formation of the John Day river, Central Oregon. Judging from the remains, it was, after the *Nimravus gomphodus* the most abundant feline of that region.

NIMRAVUS Cope

This genus has the dental formula and characters of *Hoplophonus*, with the addition of a tubercular inferior molar tooth. It is, moreover, not a true sabre-tooth, as is that genus, since it does not display the inferior anterior flange of the mandible. This is represented by an obtuse angular border, quite as in the species of *Archæolurus*, in which genus *Nimravus* finds its nearest ally. The constant absence of the anterior premolars in both jaws distinguishes it sufficiently from that genus. On this account, and in view of the larger development and denticulated edge of the superior canine teeth, *Nimravus* may be considered as occupying a position between the two genera above named.

Two species are known to me, a larger and a smaller, both from the Middle Miocene formation.

Nimravus gomphodus Cope.

The *Nimravus gomphodus* is as large as the full-grown panther of the large varieties. It probably stood as high above the ground, but whether the body had the elongate proportions of that animal, or the more robust form of the leopard and jaguar, cannot be ascertained in the absence of necessary material. Unless the animal had pendulous upper lips, a thing unknown among cats, the superior canine teeth must have been distinctly displayed on each side of the chin; their points descending entirely below the lower margin of the lower jaw, when the mouth is closed. As these points are less compressed than in the true sabre-teeths, they were less liable to fracture from lateral blows, but were more apt to be broken by fore-and-aft strains, owing to their slenderness.



FIG. 5.

FIG. 6.

FIG. 5.—End of tibia and astragalus of *Archelurus debilis*.
FIG. 6.—Femur of *Nimravus gomphodus*. All one-third natural size. Mus. Cope.

The long canines of this species testify to blood-thirsty habits, for as weapons for penetrating wounds they are without rival among carnivorous animals. They resemble considerably the teeth of some of the *Dinosauria*, for instance, those of the Triassic *Clepsysaurus*. The sectorial apparatus is especially effective, and no tissue could long resist the combined action of the opposing blades of the two jaws. Nevertheless this species did not, probably, attack the large *Merycochoeri* of the Oregon herbivores, for their superior size and powerful tusks would generally enable them to resist an enemy of the size of this species. They were left for the two species of *Pogonodon*, who doubtless held the field in Oregon against all rivals. The compressed mandibular rami of the *Nimravus gomphodus*, though less slender than those of the *Archelurus debilis*, are not so well calculated to resist lateral strains as the more robust jaws of the majority of the existing *Felidae*.

Nimravus confertus Cope.

Although a left mandibular ramus is all that I have been able to obtain of this cat, the evidence is sufficient that it is specifi-

cally different from the others enumerated in this chapter. It is inferior in size, and peculiar in the reduced symphyseal and in-



Fig. 7.—*Nimravus gomphodus*, two-fifths natural size. Mus. Cope. From Vol. IV, U. S. Geol. Surv. Terrs.

cisive parts of the mandible. It was found by Mr. Wortman in the bad-lands of the John Day valley, Oregon.

Division III. The Primitive Sabre-tooths.

DINICTIS Leidy.

With this genus we enter the group of the primitive sabre-tooths, commencing with the most generalized form. The skeleton is yet unknown, but the skull and dentition are those of a true sabre-tooth, and there seems to be no ground for believing the Musteline affinities suggested by Leidy.¹ It occupies the lowest position on the line of the sabre-tooths, on account of its numerous and simply constructed molar teeth, and stands in immediate connection with the false sabre-tooth group, having exactly the dental formula of *Elurogale* Filh. On this account I formerly united the two genera, but now believe that the absence of the inferior flange of the mandible in *Elurogale* is sufficient ground for maintaining them as distinct. The latter genus, in this respect, exactly resembles *Archæolurus* and *Nimravus*.

Remains of this genus are quite abundant in the White River

¹ Extinct Mammalia, Dak., Nebr., p. 64.

formation in Nebraska and Colorado. They principally belong to the longest known and typical species, *D. felina* Leidy. Specimens are much less numerous in the Truckee beds of Oregon. Two species have been obtained from the former horizon, the *D. felina* and *D. squalidus*, and one from the latter, the *D. cyclops*.
Dinictis cyclops Cope.

This cat is represented by a perfect cranium with its mandible, which lacks only the posterior portions. The dentition is com-



FIG. 8.—*Dinictis cyclops*, one-half natural size. Mus. Cope. From Vol. IV, U. S. Geol. Surv. Terrs.

plete, excepting the posterior parts of the two inferior sectorials, and the apices of the canines and incisors. The condition of the specimen allows its characters to be seen with clearness. The species was as large as the fully grown Canada lynx. Although of an inferior position in the system of *Carnivora*, its powers of destruction must have excelled those of the catamount. While the skull is generally less robust, its sectorial teeth are not smaller nor less effective than those of that animal, and the canines far excel those of the living species, as instruments for cutting their prey.

Dinictis felina Leidy.

This species is known from a number of crania and jaws. The former differ in their proportions from those of the *D. cyclops*, having a relatively longer cerebral and shorter facial part of the skull. The anterior premolar teeth, especially in the upper jaw, were stronger than those of *D. cyclops*.

Dinictis squalidens.

In this species the first lower molar tooth has but one root, while in the others there are two. The canine tooth of the typical specimen has also a very peculiar form. The crown is short and wide like that of a *Carcharodon* shark, or somewhat like that of the sabre-tooth *Drepanodon latidens* Owen. As the first true molar tooth of this specimen was not fully protruded, it is possible that this canine belongs to the deciduous series.

As the tubercular tooth of the specimen on which this species was established could not be found in the jaw, I proposed to regard the species as typical of a genus distinct from *Dinictis*, remarking at the time that should such a tooth be ultimately found, the genus would have to be abandoned. Evidence of the existence of this tooth was afterwards obtained. Still later, another sabre-tooth was found with precisely the formula supposed to characterize this discarded genus (*Daptophilus*). Under the circumstances I thought best to give the former a new name, *Pogonodon*.

Pogonodon Cope.

This genus represents a station on the line connecting *Dinictis* with the higher sabre-tooths, being intermediate between the former genus and *Hoplophoneus*. It lacks the tubercular inferior molar of *Dinictis*, and possesses the second inferior premolar characteristic of that genus, which is wanting in *Hoplophoneus*. One species is certainly known, and a second is provisionally referred here. The two are the largest of the sabre-tooths of North America, the type *P. platycopis* equaling in dimensions the largest species of *Drepanodon*, being only exceeded among the true sabre-tooths by the species of *Smilodon*. Unfortunately only the skull of the typical species is known. Several bones of the *P. brachyops* have been discovered.

Pogonodon platycopis Cope.

As the greater part of the skeleton of the *Pogonodon platycopis* is unknown, little can be said as to its general proportions. The skull is one-sixth shorter than that of the usual size of the tiger (*Uncia tigris*), and is equal to the largest Brazilian variety of the jaguar, and is considerably larger than the Texan form of that species.

The development of the dentition is concentrated in the canine teeth, and the powers of destruction of the animal would seem to

be disproportioned to its ability to appropriate its prey as food. The molar teeth are rather small, as is the case with the earliest

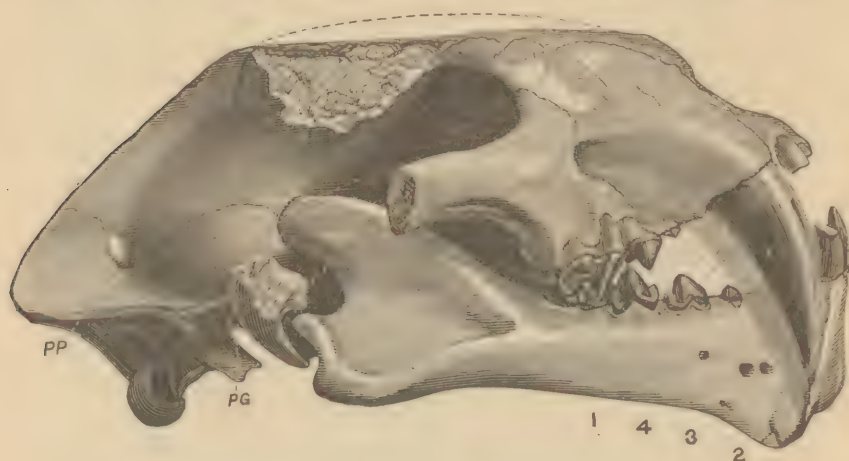


FIG. 9.—*Pogondon platycopsis*, less than two-fifths natural size. Mus. Cope.

From Vol. IV, U. S. Geol. Surv. Terrs.

representatives of the canine family. The inferior sectorial is primitive and peculiar in its robust heel. We can suppose this species to have been a great destroyer of contemporary mammalian life, and that the largest ungulates of the Truckee fauna were its victims.

History. Science has hitherto had little knowledge of this species, and owes what is here recorded to a fortunate chance. The exploring party which I had sent into the John Day River valley under the direction of Mr. Jacob L. Wortman, in 1879, examined the bad-lands in the locality known as The Cove. In passing the bluffs on one occasion, a member of the party saw on the summit of a pinnacle of the crag what appeared to be a skull. The large shining objects supposed to be teeth attracted his attention, and he resolved to obtain the specimen. He, however, was unable to climb the cliff, and returning to camp narrated the circumstance. The other men of the party successively attempted to reach the object, but were compelled to descend without it, and in one case, at least, the return was made at considerable peril. A later attempt, made by Leander S. Davis, of the party, an experienced collector, was more successful. By cutting notches with a pick, in the face of the rock, he scaled the pinnacle and brought down the skull, but at considerable risk to limb and life.

Pogonodon brachyops Cope.

This was a most formidable animal, and its dental characters indicate a high degree of efficiency of both the lacerative and of the biting functions. While the *P. platycopis* has a larger development of the canine teeth, it is inferior in the relative size of

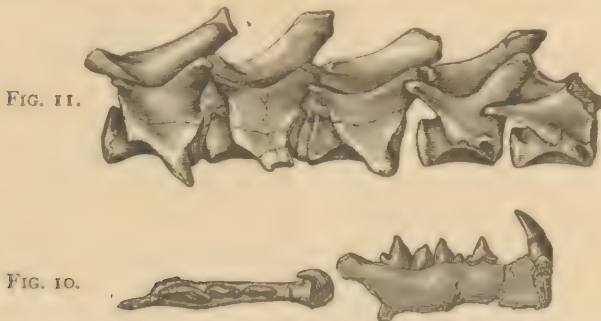


FIG. 10.—Lower jaw of *Nimravus confertus*, one-third natural size. FIG. 11.—Dorsal and lumbar vertebrae of *Pogonodon brachyops*, one third natural size. Mus. Cope. From Vol. IV, U. S. Geol. Surv. Terrs.

the sectorials. In the latter respect the *P. brachyops* resembles the species of *Nimravus* and *Archaelurus*, but these are furnished with smaller or more slender canines. It, however, resembled the latter in having the feet relatively smaller than in the recent cats, a character which indicates inferior prehensile power. Unfortunately no ungual phalanges have been preserved, so that we cannot learn whether they confirmed this indication by resembling those of the *Cynelurus jubatus* or the still less specialized forms of other families.

History. This species was the first of the Oregon felines of which bones were obtained. It was first sent here by Mr. C. H. Sternberg from the Truckee Miocene bad-lands of the John Day valley, Oregon. Although I do not possess a mandible, I am satisfied that it is more nearly allied to *Dinictis* and the present genus than to *Nimravus*. It differs from the species of that genus and *Archaelurus* in the following points: (1) the truncate triangular posttympanic process; (2) the transverse frontomaxillary suture; (3) the preorbital impressed depression; (4) the superior position of the postparietal foramen.

HOPLOPHONEUS Cope.

In this genus we reach the dental formula of *Drepanodon* and the true cats, while at the same time the primitive form of the

sectorials of the lower jaw remains. Three or four species only are known as yet, all from North America. We may expect, however, to find the genus in various parts of the world, wherever the beds occur which represent the time immediately preceding the epoch of the true sabre-tooths. The longest known species is the

Hoplophoneus primævus Leidy, from the White River bad-lands of Dakota and Nebraska. It is about as large as the Canada lynx, and has long and slender superior canines. A larger species, the *H. occidentalis* Leidy, from the same horizon and locality, is known from a single jaw fragment, as large as the corresponding part of the *Nimravus gomphodus*. Although the oldest members of the *Nimravidae* yet known from North America, the *Drepanodon* characters of the mandible and of the superior canine tooth are well developed, much more so than in the false sabre-tooth group of the later Tertiary epoch. In Europe, however, it must be remembered that the latter division commences still earlier, in the Upper Eocene, in the genus *Elurogale* Filhol.

Hoplophoneus oreodontis Cope.

This species is nearly allied to the *Hoplophoneus primævus*, of which it may be only a regional variety. It is distinguished by its shorter and wider face and palate, a character especially seen in the shortness of the diastema, which is considerably less than in the Nebraska species. With this animal it compares much as the bull-dog does with the ordinary varieties of the genus *Canis*.

The two specimens I have described were found by myself on a denuded portion of the White River formation in Northeastern Colorado. At the same locality were multitudes of bones, mostly jaws, of fifty species of various orders of *Mammalia* and *Reptilia*, on many of which it doubtless preyed.

Hoplophoneus cerebralis Cope.

This peculiar species, the smallest of the genus, approaches nearest in dentition to the true sabre-tooths (*Drepanodon*), and is represented by a skull, from which the basioccipital region, a good deal of the right side, and the lower jaw are absent. It differs in many respects from all the members of this family of cats heretofore discovered in North America. In almost every point in the osteology of the skull it is peculiar. There is not as much space for the temporal muscle as in most of the extinct

species described, or as in the large recent *Uncie*, but the points of origin of the muscle indicate that it was relatively stronger than in the domestic cat and the lynxes. Its single premolar is very small, so that the dentition for practical use is reduced, in the upper jaw, to the canine and sectorial. Both have been most effective instruments in the performance of their respective functions. The sectorial has a distinct anterior basal lobe. The space for the accommodation of the brain is relatively more ample than in any other feline of the formation, and the inner wall indicates that the convolutions of the hemispheres were well developed. This species, if the cranium were of usual proportions, was about the size of the red lynx (*Lynx rufus*).

The unique specimen of this species was found by Mr. J. L. Wortman in the bad-lands of Camp creek, one of the head tributaries of the Crooked river, in Central Oregon.

Hoplophoneus strigidens Cope.

Represented only by a part of a canine tooth. This tooth belonged to an animal of about the size of the *H. cerebralis*, and perhaps to that species. If so, it indicates for it a longer canine than usual, as its extremely compressed form points to a position at a considerable distance beyond the base of the crown. The probabilities are against reference to the *D. cerebralis*.

The tooth is the most elegant in form and perfect in its details yet found. As a cutting instrument it is superior to anything of human manufacture which I have seen.

Found by C. H. Sternberg on the John Day river, Oregon, in the Truckee beds.

FELIDÆ.

As defined in the preceding pages, the family of the true cats is of comparatively modern origin. We know that they existed during the Pliocene epoch, and it is very probable that they have been found in the Upper, and perhaps in Europe, in the Middle Miocene. If *Pseudelurus* and *Proaelurus* pertain to it, the family dates from the Upper Eocene (Phosphorites).

Like the *Nimravide*, the *Felidæ* has its sabre-tooth division, with the long superior canine, reduced interior canine, and flared lower jaw already described. In both divisions species are known which exceed in size any of those of the older family which have yet come to light. Such animals constitute the most formidable type of Carnivorous *Mammalia*.

The classification of the family is as follows :

I. The anterior and lateral faces of the mandible separated by an angle.

α . Inferior border of mandible flared downwards in front.

β . Inferior sectorial without heel ; an anterior lobe of the superior sectorial, and posterior lobes of the premolars.

Premolars $\frac{3}{2}$, first inferior two-rooted.....*Drepanodon*.

Premolars $\frac{2}{2 \text{ or } 1}$, first inferior one-rooted.....*Smilodon*.

II. The anterior and lateral faces of the mandible continuous, convex. (No inferior tubercular molar.)

α . Inferior sectorial without heel ; premolars with posterior lobes ; superior sectorial with anterior lobe.

β . Superior sectorial without internal heel ; ungual phalanges without inferior process.

Pupil round, premolars $\frac{3}{2}$; orbit open posteriorly.....*Cynalurus*.

$\beta\beta$. Superior sectorial with internal heel ; ungual phalanges with inferior process.

γ . Pupil round.

Premolars $\frac{3}{2}$*Uncia*.

Premolars $\frac{1}{2}$*Neofelis*.

$\gamma\gamma$. Pupil vertical.

Orbit closed behind ; premolars $\frac{3}{2}$*Catolynx*.

Orbit open ; premolars $\frac{3}{2}$*Felis*.

Orbit open ; premolars $\frac{1}{2}$*Lynx*.

The tendency to reduction of the number of molar teeth is seen in the above genera, as already pointed out in the *Nimravidae*.

The only extinct genera are *Drepanodon* and *Smilodon*. Of the other genera the greater number of extinct species belong to *Uncia*.

The following catalogue of species and their distribution shows that but few of the extinct *Felidae* have yet been found in North America. A star on a line between two columns shows an intermediate stratigraphical position. The extinct true cats whose crania have been discovered, belong to *Uncia*, but it is possible that some of the European species, which are as yet only known from lower jaws, may be species of the genus *Felis* or *Lynx*.

	Upper Eocene.	Lower Miocene.		Upper Miocene.		Pliocene.	
	Eur.	Eur.	Am.	Eur.	Am.	Asia. Eur.	Am.
<i>Drepanodon palmidens</i> Blv.....			×				
“ <i>ogygius</i> Kp.....			×				
“ <i>aphanista</i> Kp.....			×				
“ <i>sivalensis</i> F. and C.....						×	
“ <i>palaeindicus</i> Bose.....						×	
“ <i>megantereon</i> C. and J.....						×	
“ <i>cultridens</i> Cuv.....						×	
“ <i>maritimus</i> Ger.....						×	
“ <i>latidens</i> Ow.....						×	
<i>Smilodon neogæus</i> Lund.....							×
“ <i>necator</i> Gerv.....							×
“ <i>fatalis</i> Leidy.....							×
“ <i>gracilis</i> Cope.....							×
<i>Uncia media</i> Lart.....			×				
“ <i>attica</i> Gaudry.....				×			
“ <i>cristata</i> F. and C.....					×		
“ <i>grandicristata</i> Bose.....					×		
“ <i>christoli</i> Gerv.....					×		
“ <i>pardinensis</i> C. and J.....					×		
“ <i>arvernensis</i> C. and J.....					×		
“ <i>brevirostris</i> C. and J.....					×		
“ <i>issiodorensis</i> C. and J.....					×		
“ <i>augusta</i> Leidy.....							×
“ <i>atrox</i> Leidy.....							×
“ <i>spelæa</i> Gf.....						×	
“ <i>longifrons</i> Burm.....							×

As already remarked, the genera of the Nimravine and Drepanodont lines are extinct, and this in spite of the fact that they presented the most perfect weapons of destruction in their canine teeth, from the earliest times. Their other modifications of structure advanced, *pari passu*, with those of the feline series, and, among others, the feet presented in the latter forms at least (*e. g.*, *Smilodon necator*, Gerv.), the most perfect prehensile power of the lions and tigers of to-day. As nothing but the characters of the canine teeth distinguished these from the typical felines, it is to these that we must look for the cause of their failure to continue. Prof. Flower's suggestion appears to be a good one, viz: that the length of these teeth became an inconvenience and a hindrance to their possessors. I think there can be no doubt that the huge canines in the *Smilodons* must have prevented the biting off of flesh from large pieces, so as to greatly interfere with feeding, and to keep the animals in poor condition. The size of the canines is such as to prevent their use as cutting instruments, excepting with the mouth closed, for the latter could not have been opened sufficiently to allow any object to enter it from the front.

Even when it opens so far as to allow the mandible to pass behind the apices of the canines, there would appear to be some risk of the latter's becoming caught on the point of one or the other canine, and forced to remain open, causing early starvation. Such may have been the fate of the fine individual of the *S. neogaeus*, Lund, whose skull was found in Brazil by Lund, and which is familiar to us through the figures of De Blainville, etc.

DREPANODON Nesti. (*Machærodus* Kaup).

This genus as understood by most authors, belongs to the later Miocene and Pliocene, and has had numerous representatives in Europe and Asia. No species has as yet been found in America. Some of the species described by authors are only known from fragments, so that much remains to be ascertained as to the prevalence among them of the characters I have assigned to the genus and family. Those given are derived from the two species best known, the *D. cultridens* and *D. meganteron*, which have been readily obtained from the descriptions and figures of authors.

It is difficult to ascertain the number of European species. Pomel's catalogue is generally cited, and this is, with some subtractions and additions, the basis of the list already given.

SMILODON Lund.

Besides the family characters already given, this genus differs from the *Nimravide* in two other important respects. In both points it differs also from such existing members of the *Felide* with which I have been able to compare it. In both *S. fatalis* and *S. necator*, the posttympanic process of the skull is coössified with the postglenoid, thus closing the auricular meatus below. It thus differs from other *Felide* as the genus *Rhinoceros* differs from various other members of *Rhinoceride*. The second point has been indicated by Prof. Gervais. There is no epitrochlear arterial canal, such as belongs to cats and *Nimravide* generally. This I have only verified on the *S. necator*.

This genus represents in America the Drepanodons of the Old World. The known species belong to the Pliocene period, and were the cotemporaries of the gigantic sloths and *Glyptodons*, which at that time ranged over the entire American continent. Their powerful limbs terminated by immense claws, bespeak for them exceptional force in striking and tearing their prey, and the long compressed canine teeth are well adapted for penetrating the

tough hides and muscles of the large Edentata, which were doubtless their food. There are known two species of large size from



FIG. 13.—*Neotoma neotoma* Gervais, one third natural size. Original. Mus. Cope.

the Pliocene of South America, and probably two species from North America. A figure of the skeleton of the *S. neotoma* Gervais accompanies this paper. It is a copy of a lithograph taken by Prof. Burmeister from a specimen in the Museum of Buenos Ayres. The second known skeleton, found by M. Larroque near to the village Arco, a few miles west of Buenos Ayres, is in possession of the writer. Lateral and inferior views

of the skull of this individual, one-third of the natural size, are represented in figures 13 and 14.



FIG. 14.—*Smilodon necator*, one-third natural size. Inferior view of skull Fig. 12.

This specimen is the one on which the late Prof. Gervais based his determination of the species (*Comptes Rendus*, 1878, June), but which he had not described at the time of his death. The species is about the size of the lion, and of the most formidable character.

A fragment of a maxillary bone containing a sectorial tooth found in Texas was referred to an extinct cat, by Prof. Leidy, under

the name of *Trucifelis fatalis*. As it possesses a second anterior basal lobe of the superior sectorial, it is doubtless a *Smilodon*. I am confirmed in this opinion by the characters presented by an important specimen sent me by G. W. Marnock, who obtained it in Southwestern Texas. It consists of that portion of a cranium, which is posterior to the orbits, and represents an animal of the size of the *S. necator*, or of a large tiger. The positions of the foramina and the conjunction of the posttympanic and postglenoid processes are as in the *S. necator*. When more of this species is known, it will doubtless be found to be our largest sabre-tooth.

Among the remains obtained by Charles M. Wheatley from a cave on the Schuylkill river, in Pennsylvania, which I described in 1871, there occurred a part of the canine of a sabre-tooth. Hoping to obtain better specimens, I did not include it in the published lists. Having established the existence of the genus *Smilodon* as a contemporary of the sloths during the Pliocene period in North America, it becomes probable that the species of the caves is also to be referred to it. The canine in question has lost most of its crown. It is of smaller size than that of either of the three species previously mentioned, and its basal portion is more compressed. This compression is a marked character, and I refer to it the name *Smilodon gracilis*, by which the species may be known.

UNCIA Gray (Cope emend.).

Extinct species of this genus have been found in the late Miocene and subsequent deposits in India, Europe and North America. It is distinguished from the

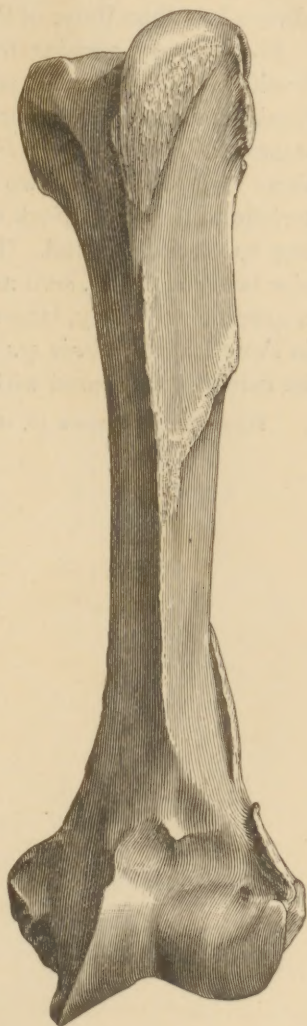


FIG. 15. — *Smilodon necator*; humerus of specimen Figs. 12, 13, from front, one-third natural size. Mus. Cope.

true *Felis* by the round form of its pupils. This can only be observed in the living species, so that some correlated index of it must be used in determining the genus from skulls. This Dr. Gray shows is seen in the small size of the orbits, which are always less than those of the species of *Felis*.

Fragmentary remains from the Loup Fork formation of Nebraska and the Pliocene and Quaternary of Mississippi and California have been described by Leidy under the names of *Felis augustus*, *F. atrox* and *F. imperialis*. Dr. Leidy suggests that there may have been two species, the one (*F. augustus*) characteristic of the Loup Fork epoch, and *F. atrox*, the second, belonging to a later period. The *Uncia augusta* was intermediate in size between the *U. onca* and the tiger, while the *Uncia atrox* was, according to Leidy, larger than the lion or tiger. It represents in America the *Uncia spelea* of the European caves, and should be carefully compared with that species.

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